

1 **A REVIEW OF DIAPAUSE AND TOLERANCE TO EXTREME TEMPERATURES IN DERMESTIDS**
2 **(COLEOPTERA)**

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5 **D.M. Wilches^{a,b}, R.A. Laird^b, K.D. Floate^a, P.G. Fields^{c*}**

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7 ^a Lethbridge Research and Development Centre, Agriculture and Agri-Food Canada, Lethbridge, AB T1J
8 4B1, Canada

9 ^b Department of Biological Sciences, University of Lethbridge, Lethbridge, AB T1K 3M4

10 Canada

11 ^c Morden Research and Development Centre, Agriculture and Agri-Food Canada, Winnipeg, MB R3T
12 2M9, Canada

13

14 * Corresponding author: Paul.Fields@agr.gc.ca.

15 **Abstract**

16 Numerous species in Family Dermestidae (Coleoptera) are important economic pests of stored
17 goods of animal and vegetal origin, and museum specimens. Reliance on chemical methods for
18 of control has led to the development of pesticide resistance and contamination of treated
19 products with insecticide residues. To assess its practicality as an alternate method of control,
20 we review the literature on the tolerance of dermestids to extreme hot and cold temperatures.
21 The information for dermestid beetles on temperature tolerance is fragmentary, experimental
22 methods are not standardized across studies, and most studies do not consider the role of
23 acclimation and diapause. Difficulties in determining the diapause status of dermestid larvae
24 may explain the lack of studies. The few studies that do examine these factors show that they
25 can greatly increase tolerance to cold temperatures. The use of extreme temperatures will
26 need to target the most tolerant life stage, which for dermestids at cold temperatures will
27 potentially be the cold-acclimated individuals in diapause. The development of effective
28 protocols will be facilitated by studies that clearly and completely describe experimental and
29 statistical methods, consider factors (life-stage, acclimation, diapause) that increase tolerance
30 to extreme temperatures, and assess the mortality at various temperatures to develop
31 mathematical models.

32

33 **Keywords:** *Trogoderma*, museum pests, stored-product pests, Dermestidae, thermal control

34 **1. INTRODUCTION**

35 Dermestid beetles (Coleoptera: Dermestidae) comprise a diverse group of more than 1200
36 described species in 45 genera. Most species are xerophilous necrophages; i.e., they develop on
37 the desiccated tissues and hairs of dead animals (Háva & Nardi, 2004; Kiselyova & Mchugh,
38 2006; Zhantiev, 2009) (Table 1). Necrophagus species (e.g., *Dermestes* spp.) feed in animal
39 carcasses and on dead insects (Kingsolver, 2002; Zhantiev, 2009). Nidicolous species (e.g.,
40 *Anthrenus* spp.) occur on mammals and in bird nests, where they feed on hair or feathers
41 (Peacock, 1992; Háva, 2004; Zhantiev, 2009). A small number of species are predators and feed
42 on wasp and bee larvae, and on spider eggs (Zhantiev, 2009). Feeding on plants is atypical for
43 the family, but their tolerance to low humidity allows some dermestids (mainly *Trogoderma*
44 spp. and *Attagenus* spp.) to develop solely on dried cereal products (Hinton, 1945; Kiselyova &
45 Mchugh, 2006; Zhantiev, 2009).

46 A number of dermestids are of key economic importance. Some genera (*Trogoderma*,
47 *Attagenus*) are pests of stored grains and stored grain products (Hinton, 1945; OEPP/EPPO,
48 2013). Other genera (*Attagenus* spp., *Anthrenus* spp.) are common in museums, where they
49 damage preserved insect, bird, and mammal specimens, or items that contain plant or animal
50 materials (Pinniger, 1991; Veer *et al.*, 1991; Linnie, 1994). Species of *Anthrenus*, *Anthrenocerus*
51 and *Dermestes* develop in products that contain wool, cotton, linen, synthetic fibres, and silk
52 (Bennet *et al.*, 1988; OEPP/EPPO, 2013). Species of *Attagenus* and *Dermestes* consume
53 silkworm cocoons and prey on different life stages of silkworms (Kumar *et al.*, 1988; Veer *et al.*,
54 1996). About 28 species of *Dermestes* infest stored silkworm cocoons and *D. maculatus* is a
55 reported vector of the microsporidian *Nosema bombycis* Nageli, which is the causative agent of
56 pébrine disease in silkworms (Veer *et al.*, 1996). Dermestids also infest the packaging and
57 containers used to ship stored products which, in combination with international commerce,
58 have contributed to the cosmopolitan distribution of many dermestid species (Willey &
59 Wayman, 1979; Turner, 1986).

60 Given their economic importance, there is a large body of research describing measures to
61 control dermestid infestations. Control, however, is complicated by the ability of some
62 dermestids to undergo diapause. This ability is uncommon among stored-product insects and
63 increases the tolerance of dermestids to extreme climatic conditions and insecticides (Bell,
64 1994).

65 **Table 1.** Biology and life history of the most economically important species of dermestids.

66

Species	Common name	Geographic distribution	Temperature (°C) ^a	RH (%) ^a	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
<i>Anthrenus coloratus</i> (Reitter 1881)	Asian carpet beetle	Southeast Europe, England, USA, Africa, Asia	33-35	70-80	6-9	115 -120 (univoltine)	-	Yes	Stored product and museum specimen pest	Ali (1997)
<i>Anthrenus flavipes</i> (LeConte 1854)	Furniture carpet beetle	Nearly cosmopolitan	35	90	18-20	246-248 (bivoltine)	-	Yes (obligate)	Animal products, museum pests	Griswold & Greenwald (1941); Ayappa <i>et al.</i> , (1957)
<i>Anthrenus sarnicus</i> (Mroczkowski 1963)	Guernsey carpet beetle	Europe	25	70	8	337	28	Yes (obligate)	Pest of dried animal collections in museums	Coombs & Woodroffe (1983); Armes (1988)
<i>Anthrenus verbasci</i> (Linnaeus 1767)	Varied carpet beetle	Cosmopolitan	20	70	3-5	192	27	Yes (obligate)	Pest of dried insect collections/silkworms pupae	Griswold & Greenwald (1941); Blake (1958)
<i>Anthrenocerus australis</i> (Hope 1843)	Australian carpet beetle	Europe and Australia	25	60-70	5-6	246	30	Yes (obligate)	Pest of dried dairy products, wool and other fabrics	Gerard & Ruf (1997)
<i>Attagenus augustatus</i> (Ballion, 1871)	-	China, Russia, middle east and India	29	-	-	730 (biennial)	150- 300	-	Pest of textiles, woolen fabrics and grains	Veer & Rao (1995)

Species	Common name	Geographic distribution	Temperature (°C) ^a	RH (%) ^a	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
<i>Attagenus cyphonoides</i> (Reitter 1881)	-	Nearctic, Oriental and Palaearctic regions	22-27	45-70	-	118-132 (univoltine)	10-14	Yes (obligate), larvae overwinter	Woolen and other animal products	Veer <i>et al.</i> , (1991)
<i>Attagenus elongatulus</i> (Casey 1900)	"yellow" black carpet beetle	Palaearctic region	27	50-70	-	90-95 days	18-20	Yes (crowded)	Infests plant and animal materials: woolens, felt and processed foods	Barak & Burkholder (1977)
<i>Attagenus indicus</i> (Kalik 1954)	-	India, Nepal	27	75	-	240-270 days (univoltine)	144-229	Hibernates as larvae or adult	Stored woolen fabrics and carpets	Veer & Rao (1995)
<i>Attagenus unicolor</i> (Brahm 1790)	Black carpet beetle	Cosmopolitan	28	65	5-11	> 326	3-35	Yes (obligate and larval crowding)	Pest of dead animal and vegetal materials	Back & Cotton (1938); Griswold & Greenwald (1941); Baker (1977, 1982)
<i>Attagenus fasciatus</i> (Thunberg 1795)	Banded black carpet beetle	Europe, nearly cosmopolitan	35	80	8-14	136 (bivoltine)	26-30	-	Attacks animal and vegetal products in storage	Ali <i>et al.</i> , (2011)
<i>Attagenus lobatus</i> (Rosenhauer 1856)	-	North Africa, South Europe, USA, Asia	25-27	65-70	-	253-287 (univoltine)	78-112	Overwinters as larvae or pupae	Woolen products	Veer <i>et al.</i> , (1991)
<i>Attagenus scalaris</i> (Pic 1893)	Black carpet beetle	Egypt, Libya	30	50	8-22	90-385	17-28	-	Stored textiles of animal origin	Abdel-Rahman, <i>et al.</i> , (1981)

Species	Common name	Geographic distribution	Temperature (°C) ^a	RH (%) ^a	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
<i>Attagenus smirnovi</i> (Zhantiev 1973)	Brown carpet beetle	Europe, Africa	20	65	-	22-32	20	Yes	Animal and vegetal museum collections	Hansen <i>et al.</i> , (2012)
<i>Dermestes ater</i> (Degeer 1774)	Black larder beetle	Cosmopolitan	25	40-80	-	64-77	100-200	-	Pest on raw animal products	Coombs (1981)
<i>Dermestes haemorrhoidalis</i> (Küster 1852)	Black larder beetle, sheepskin dermestid	Nearly cosmopolitan	25	65	-	95-112	110-194	-	Animal and vegetal products, insect collections	Coombs (1979)
<i>Dermestes lardarius</i> (Linnaeus 1758)	Larder beetle	Cosmopolitan	25	65	7	48-50	244	-	Scavengers/animal products	Coombs (1978); Jacob & Fleming (1984)
<i>Dermestes maculatus</i> (DeGeer 1774)	Leather (Hide) beetle	Cosmopolitan	33	-	6-8	34-40	14	Yes (crowded)	Stored produced of animal and vegetal origin	Osuji (1975); Cloud & Collison (1986)
<i>Dermestes peruvianus</i> (LaPorte de Castelnau 1840)	Peruvian larder beetle	South America, USA, Europe, Asia	25	65	-	65-73	33-192	-	Plant and animal material	Coombs (1979)

Species	Common name	Geographic distribution	Temperature (°C) ^a	RH (%) ^a	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
<i>Trogoderma anthrenoides</i> (Sharp 1902)	-	America, Europe, Asia	35	70	-	41-46	7-10	Yes (isolation)	Pest of plant and animal stored-products and museum specimens	Burges & Camell (1964)
<i>Trogoderma variabile</i> (Ballion 1878)	Warehouse beetle	Europe, Nearctic	32	70	5-6	30-46	14	Yes (isolation)	Pest of stored grain	Loschiavo (1960); Partida & Strong (1975)
<i>Trogoderma granarium</i> (Everts 1898)	Khapra beetle	Europe, Asia and Africa	35	73	4-7	24-36	12-14	Yes (crowded, isolation)	Major pest of animal and vegetal stored products (mainly grain and cereals)	Hinton (1945); Hadaway (1955); Burges (1962b)
<i>Trogoderma versicolor</i> (Creutzer 1799)	European larger cabinet beetle	Palaeartic region	30	73	-	30-43	12-16	-	Pest of dried animal and vegetal products/insect collections	Hadaway (1955)
<i>Trogoderma inclusum</i> (LeConte 1854)	Larger cabinet beetle	Nearly cosmopolitan	35	73	4-7	36-42	3-16	Yes (isolation)	Minor stored product pest	Strong (1975); Klein & Beck (1980)
<i>Trogoderma angustum</i> (Solier 1849)	Cabinet beetle	America, introduced to Asia and Europe	-	-	-	-	-	Yes (isolation)	Textiles and insect collections	Bell (1994)
<i>Trogoderma sternale</i> (Jayne 1882)	Cabinet beetle	Nearctic	-	-	-	-	-	Yes (isolation)	Minor stored product pest	Bell (1994)

Species	Common name	Geographic distribution	Temperature (°C) ^a	RH (%) ^a	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
<i>Trogoderma glabrum</i> (Herbst 1783)	Glabrous carpet beetle	Holarctic region (temperate)	27-38	-	5-6	30-49	6-14	Yes (isolation)	Minor stored product pest	Beck (1971a); Archer & Strong (1975); Klein & Beck (1980)
<i>Trogoderma ornatum</i> (Say 1825)	Ornate cabinet beetle	Neartic region	-	-	-	-	-	Yes	Minor stored product pest	Bell (1994)
<i>Trogoderma simplex</i> (Jayne 1882)	Plain cabinet beetle	USA and Canada	32	50	5-6	63-77	10-22	Yes (isolation)	Minor stored product pest	Strong & Mead (1975)
<i>Trogoderma grassmani</i> (Beal 1954)	Tiny cabinet beetle	USA and Canada	-	-	-	-	-	Yes (isolation)	Minor stored product pest	Bell (1994)

*Blank cells represent unavailable information

^aTemperature and humidity for the reported developmental time (days)

67 Control primarily has relied on fumigants and contact insecticides. Fumigants that have been
68 used to control dermestids include methyl bromide (Lindgren & Vincent, 1959; Linnie, 1994;
69 Fields & White, 2002; MBTOC, 2010), phosphine (Vincent & Lindgren, 1972; Bell *et al.*, 1984;
70 Udeaan, 1990; Linnie, 1994; Bell & Wilson, 1995; Farooq *et al.*, 2000; Ahmedani *et al.*, 2007),
71 naphthalene (Linnie, 1994), p-dichlorobenzene (Linnie, 1994), and sulfuryl fluoride (Su &
72 Scheffrahn, 1990; Rajendran *et al.*, 2008; Sriranjini & Rajendran, 2008). Contact insecticides
73 used to control dermestids include malathion (Lindgren & Vincent, 1959; Singh & Yadav, 1994;
74 Khosla *et al.*, 2005), pyrethrins (Linnie, 1994), and chlorpyrifos (Singh & Yadav, 1994; Khosla *et*
75 *al.*, 2005; Eliopoulos, 2013). Use of fumigants and contact insecticides promote the
76 development of resistance, introduce residues into the environment, and can be detrimental to
77 the consumer's health (Cao *et al.*, 2002; Rajendran, 2002; Rajendran & Parveen, 2005). Methyl
78 bromide is an ozone-depleting substance. In accordance with the Montreal Protocol, its use has
79 been generally banned on a global basis with some exemptions (MBTOC, 2010) such as
80 quarantine. Phosphine is less effective than methyl bromide and some dermestids (e.g., *T.*
81 *granarium*) already have evolved phosphine resistance (Vincent & Lindgren, 1972; Bell *et al.*,
82 1984; Rajendran, 2002). These issues have led to examination of non-chemical methods of
83 control, varying with the nature of the infested product (Rajendran & Parveen, 2005).
84 Alternative methods include the use of controlled atmospheres (CO₂-rich, O₂-poor
85 atmospheres) (Khatoon & Heather, 1990; Reichmuth *et al.*, 1993), vegetable oils (Traynier *et al.*,
86 1994), inert dust (Nakamoto, 1989), radiation (Khatoon & Heather, 1990), and extreme
87 temperatures (Fields & White, 2002; Wright *et al.*, 2002; Abdelghany *et al.*, 2015).

88 The use of extreme temperatures may provide the most viable alternative to chemical
89 applications. It has been used as an insect control method in North America since the early
90 1900s (Dean, 1911; Mathlein, 1961; Burges & Burrell, 1964), there are no reported cases of
91 insects developing resistance to heat or cold, there are no residues to harm consumers, and it
92 does not require registration, as do insecticides in most jurisdictions (Fields & White, 2002;
93 Eliopoulos *et al.*, 2011; Fields *et al.*, 2012). However, adoption of extreme temperatures as a
94 treatment method has been hampered by an inability to increase or decrease temperatures
95 economically and quickly, as well as a lack of knowledge on the combination of temperature

96 and period of exposure that is needed to control different species of dermestids (Strang, 1992;
97 Bergh *et al.*, 2006). Some of the studies that report on the thermal-mortality limits for insect
98 pests in museums are based on experience rather than on controlled experiments (Linnie,
99 1999). Furthermore, much of the literature on the temperature tolerance of dermestids is
100 difficult to access and (or) not recent (Fields, 1992; Linnie, 1999).

101 Our objectives are three-fold, we first review the literature on the tolerance of dermestid
102 beetles to extreme temperatures, discuss factors that influence this tolerance, and examine the
103 potential for extreme temperatures to control dermestids in different situations; e.g., museum
104 specimens, stored-grain products. This information will facilitate the development of standard
105 protocols to encourage adoption of extreme temperatures for use in the control of dermestid
106 pests.

107 **2. MECHANISMS OF TEMPERATURE TOLERANCE**

108 Temperature influences almost every aspect of insect biology. Temperature affects metabolic
109 rates, defines limits of physiological function, determines developmental times, impacts
110 behaviour, and ultimately influences survival of the population (Lee, 1991; Bhargava *et al.*,
111 2007). For stored-product insects, optimal temperatures maximize fitness and population
112 growth. Stored-product insects require a high minimum temperature before they can complete
113 their development. In general, temperatures above 15°C are needed for egg-laying and optimal
114 temperatures range between 25- 35°C (Fields, 1992; Strang, 1992). Suboptimal temperatures
115 (35 - 40°C and 13 - 25°C) allow completion of life cycles and reproduction, but populations
116 merely persist rather than thrive. Lethal temperatures (above 40°C and below 13°C) eventually
117 cause population extinction (Fields, 1992; Wellheiser, 1992; Bhargava *et al.*, 2007). Different
118 species can have slightly different temperature responses (Hadaway, 1955; Loschiavo, 1960;
119 Coombs, 1981; Burges, 2008; Riaz *et al.*, 2014). Cold and heat-tolerance refers to the capacity of
120 an organism to survive or tolerate exposure to temperatures and exposure times that are
121 otherwise suboptimal or lethal (Lee, 1991).

122 **2.1 Mechanisms of cold tolerance**

123 Exposure to cold can damage insect cell membranes, cause the loss of ion homeostasis, reduce
124 metabolic rates, and mechanically damage tissues (Fields, 1992; Lee, 2010). Insects enhance
125 their cold-tolerance with use of behavioural, biochemical, and physiological strategies. In
126 general, insects are classified as freeze-intolerant (die when frozen) or freeze-tolerant (capable
127 of surviving ice in their bodies) (Fields, 1992; Lee, 2010). Other systems of classification have
128 been proposed that take into consideration the different aspects of cold mortality, but these
129 have not been widely used (Nedved, 2000). All dermestids and stored-product or museum
130 collection insect pests studied to date are freeze-intolerant, and die at their supercooling point
131 (SCP), which in general range from -10 to -20°C (Evans, 1987; Strang, 1992; Fields *et al.*, 1998;
132 Linnie, 1999; Fields, 2001; Fields, *et al.*, 2012). There is significant mortality at temperatures
133 warmer than the SCP, with warmer temperatures causing less mortality (Fields, 1992; Strang
134 1992).

135 **2.2 Mechanisms of heat tolerance**

136 Exposures to sublethal high temperatures increases metabolic rates followed by the cessation
137 of movement. Prolonged exposure can change the fluidity of cell membranes, alter ionic
138 balance, and alter the structure of macromolecules to affect cell structure and the rate of
139 metabolic reactions (Fields, 1992; Nedved, 2000; Hansen *et al.*, 2011). High temperatures can
140 also increase the permeability of the cuticle wax complex causing water loss and desiccation
141 (Nedved, 2000). Heat damage is normally irreversible and, even if the insect survives heat
142 exposure, it may fail to complete development or reproduce when returned to optimal
143 temperatures (Fields, 1992; Denlinger & Yocum, 1998; Nedved, 2000; Hansen *et al.*, 2011). To
144 achieve heat tolerance, heat shock or stress proteins replace the production of normal proteins,
145 which reduce the damage to susceptible proteins (Denlinger & Yocum, 1998). Previous studies
146 show that all life stages of dermestids and some other stored-product insects can survive at
147 38°C, but most of them will be killed by an exposure of 2 hours at 50°C (Michelbacher, 1953;
148 Lindgren & Vincent, 1959; Evans, 1987; Fields, 1992; Phillips & Throne, 2010; Fields *et al.*,
149 2012).

150

151 **3. FACTORS AFFECTING THERMAL TOLERANCE**

152 Tolerance to extreme temperatures is highly variable within and among species due to multiple
153 factors (Lee, 1991; Fields, 2001). Identifying these factors is critical when designing thermal
154 treatments for the control of pest insects, particularly those life stages and species that are
155 most tolerant (Beckett *et al.*, 2007). Factors that affect temperature tolerance include: i) life
156 history of the species, ii) stage of development, iii) diapause, iv) relative humidity, v)
157 acclimation, and vi) temperature and duration of exposure (Salt, 1958; Evans, 1987; Lee, 1991;
158 Fields, 1992; Fields, 2001; Beckett *et al.*, 2007).

159 **3.1 Life history of the species**

160 The environmental conditions normally experienced by a species often define its thermal
161 tolerance (Chown, 2001). For example, insects not normally found at cold temperatures usually
162 cannot tolerate sub-zero temperatures and may die after even a brief exposure to suboptimal
163 temperatures (Salt, 1961; Doucet, *et al.*, 2009). Most granivorous species are tropical or sub-
164 tropical species able to breed rapidly over a fairly wide range of temperatures. In general,
165 however, they are more susceptible to low temperatures compared to species of insects from
166 temperate and cold zones (Burgess & Burrell, 1964).

167 **3.2 Stage of development**

168 Thermal tolerance differs among developmental stages mainly due to their physiological
169 differences (Salt, 1958; Fields, 1992; Danks, 1996, 2005, 2006; Beckett *et al.*, 2007). Life stages
170 of smaller size and lower water content have lower supercooling points. The digestive tract of
171 non-feeding life stages (e.g., pupae) do not contain food particles (which can act as ice-
172 nucleators) and, therefore, have lower SCPs than feeding stages (Denlinger, 1991; Lee, 1991).
173 Different life stages also may be associated with different microhabitats, which can affect SCPs,
174 freezing capacity, and loss of water (Denlinger, 1991; Fields, 1992). A lower SCP does not
175 necessarily mean a higher cold-tolerance, for example eggs often have low SCP but are not the
176 most cold-tolerant stage (Fields, 1992). However, within a given life stage, SCPs can often be
177 correlated with cold tolerance (Fields, 1992; Abdelghany *et al.*, 2015).

178 **3.3 Diapause**

179 Diapause is an endocrine-mediated dormancy characterized by an arrest in development and
180 suppression of metabolism that may either be obligate or facultative (Denlinger, 1991; Bell,
181 1994). For insects with obligate diapause, each individual passes through diapause regardless of
182 the external conditions (Tauber *et al.*, 1986; Kostál, 2006). For insects with facultative diapause,
183 diapause is initiated, maintained, and terminated by external cues. Thus, depending upon
184 environmental conditions, a given generation of an insect may or may not enter diapause
185 (Tauber *et al.*, 1986; Kostál, 2006). Nair and Desai (1973a) showed that strains of *T. granarium*
186 that had a facultative diapause that was induced by crowding, prevented by isolation, and could
187 be selected so that there was no diapause under crowded conditions. In other words, they
188 produced a non-diapausing strain. Also a strain could be selected so that almost all larvae in
189 both crowded (diapausing) and isolated (non-diapausing) conditions entered into diapause. In
190 other words, they produced a strain with obligatory diapause. Their finding suggests that
191 diapause is determined by multiple genes (Burgess, 1962b; Nair & Desai, 1973b). It also indicates
192 that laboratory strains could lose the ability to diapause depending upon the method of rearing
193 and generations in culture. If time is a confounding factor, tests performed over several
194 generations on the characteristics of diapause (induction, maintenance and termination) may
195 lead to erroneous conclusions if the correct controls are not present.

196 Insects entering diapause undergo physiological changes that enhance the accumulation of
197 metabolic reserves and reduce rates of energy and oxygen consumption (Tauber *et al.*, 1986;
198 Denlinger, 1991). This is achieved by the activation of diapause-specific genes that encode for
199 proteins, which affect heat shock, energy metabolism and storage, hormonal regulation, and
200 clock proteins, that influence diapause induction (Kostál, 2006). Mechanisms for diapause-
201 induction and cold tolerance may interact; i.e., both are regulated by the juvenile hormone and
202 both include the production of cryoprotectants, elimination of gut contents, and dehydration of
203 body tissues (Lindgren & Vincent, 1959; Bell *et al.*, 1984; Tauber *et al.*, 1986; Danks, 1996, 2005,
204 2006). However, the relation between diapause and cold-tolerance is not always clear. Both are
205 dynamic processes and, even within a species, some elements of diapause and cold-tolerance

206 are linked whereas others are not (Danks, 2005, 2006). Also, depending upon the species, the
207 co-occurrence of diapause and cold-tolerance may be coincidental or reflect independent
208 responses to similar inductive cues. In addition, cold-tolerance may occur in the absence of
209 diapause (and vice versa) and may increase with acclimation (Tauber *et al.*, 1986; Denlinger,
210 1991; Danks, 2005, 2006).

211 Diapause can provide higher tolerance to detrimental conditions and can improve survival to
212 extreme environments in some dermestids. The ability to undergo diapause as larvae evolved
213 to tolerate suboptimal conditions where the food supply is sporadic and unpredictable. Because
214 of this, the diapause stage allowed higher survival in their ancestral environments as scavengers
215 and in the invasion of a new niche as stored-product pests (Beck, 1973; Armes, 1988, 1990).
216 Diapause allows individuals to synchronize development within populations and to survive
217 conditions of extreme temperatures, desiccation and, increases resistance to fumigants such as
218 phosphine and methyl bromide (Burgess, 1962b; Tauber *et al.*, 1986; Pullin, 1996). When
219 conditions become conducive for growth and reproduction, the diapause stage terminates,
220 allowing for a rapid increase in the population. For example, adults of *T. granarium* that went
221 through diapause are larger and laid more eggs than the ones that didn't, promoting in that
222 way, a rapid increase of the population after diapause (Karnavar, 1972).

223 Most dermestids that diapause, do so as larvae. Some have obligate diapause, while others
224 have facultative diapause (Table 1). The genera *Anthrenus* and *Attagenus*, which are more
225 closely associated to the ancestral environments, have long life cycles (1-3 years) with a clear
226 stage of obligate larval diapause that enhances overwinter survival (Bell, 1994). For example,
227 *Anthrenus verbasci* can have 2 periods of diapause, first as early instar larvae and second as
228 mature larvae (Blake, 1958, 1959). *Anthrenus sarnicus* and *Anthrenus flavipes*, undergo
229 diapause as mature larvae only (Griswold & Greenwald, 1941; Armes, 1988, 1990). In these
230 three species, diapause is controlled by an "internal clock", all individuals go through diapause,
231 but the timing and duration of diapause can be affected by photoperiod and temperature
232 (Blake, 1958, 1959; Armes, 1988, 1990).

233 Facultative diapause is present mainly in *Trogoderma* spp. and is defined mainly as a density-
234 dependent phenomenon. During this stage the individual stay as mature larvae that feed and
235 moult occasionally, that can be identified by a low respiration rate (Beck 1971a) and a longer
236 larval stage (Burgess, 1959, 1960, 1962a, 1962b; Nair & Desai, 1972, 1973a, 1973b). This stage is
237 induced by factors that can act alone or in combination, such as exposure to low temperatures,
238 inadequate food, rearing at low or high densities (Burgess 1962b; Nair & Desai, 1972, Table 1).
239 The diapause induced by larval crowding has been widely studied in *T. granarium*, but a similar
240 facultative diapause has been described in *Attagenus elongatulus* (Barak & Burkholder, 1977),
241 *Attagenus unicolor* (Baker, 1977), and *Dermestes maculatus* (Osuji, 1975). This type of diapause
242 is terminated by a rapid increase in temperature after exposure to low temperatures. When
243 larvae undergo diapause as a result of crowded conditions, the renewal of food has little effect
244 on termination and is effective only when accompanied by isolation (Burgess, 1962a; Nair &
245 Desai, 1973a). In contrast, larvae of *T. glabrum* and *T. variabile* have a facultative diapause
246 defined as density-independent. The density-independent diapause is triggered by short
247 photoperiods, low temperatures, small food volumes, isolation (not by crowding) or
248 disturbance of the larvae (Loschiavo, 1960; Burgess, 1961, Wright & Cartledge, 1994;
249 Abdelghany *et al*, 2015). The termination of the density-independent diapause can be
250 spontaneous or follow changes in density of larvae, a rapid increase in temperature,
251 photoperiod, or the presence of pupae (Loschiavo, 1960; Burgess, 1961; Beck 1971a, 1971b;
252 Wright & Cartledge, 1994).

253 The type of dormancy seen in dermestids has generated disagreement, because it is different
254 than most insects (Tauber *et al.*, 1986; Bell, 1994). For example, larvae of *Trogoderma* spp.
255 occasionally move, feed and moult during dormancy (Burgess, 1959, 1960; Nair & Desai, 1972;
256 Barak & Burkholder, 1977; Bell, 1994). Beck (1971a) suggested that these larvae should not be
257 considered in diapause. Burgess (1959) questioned whether *T. granarium* is in quiescence or in
258 diapause when dormant. Future studies should, in particular, identify triggers for induction and
259 termination of diapause, and develop methods to better identify diapausing individuals.

260 **3.4 Relative humidity**

261 Dermestid beetles are xerophilous (thrive in dry environments) and are able to survive feeding
262 on food with water content below 10% (Zhantiev, 2009). This likely reflects the use of water
263 obtained from metabolism, the absorption of water from the air, and (or) other strategies
264 (Hinton, 1953 cited in Zhantiev, 2009; Edney, 1971; Zhantiev, 2009).

265 Lack of water can also enhance insect mortality at extreme temperatures (Convey, 2000;
266 Everatt *et al.*, 2014). The mechanisms of injury caused by extreme temperatures and
267 desiccation are similar in terms of osmotic stress and elicit similar responses for survival
268 (Convey, 2000). Low relative humidity can reduce cold tolerance in other stored-product insects
269 such as *Cryptolestes ferrugineus*, *Oryzaephilus surinamensis*, *Rhyzopertha dominica*, *Sitophilus*
270 *granarius*, *S. oryzae* and *Tribolium castaneum* (Evans, 1983; Fields, 1991). Similarly, at
271 temperatures between 40- 55°C, low humidity (< 50% RH) greatly reduces survival (Fields, 1992;
272 Beckett *et al.*, 2007), but humidity has less effect on mortality at higher temperatures.

273 **3.5 Acclimation**

274 Acclimation is a phenomenon whereby insect survival at extreme temperatures is enhanced by
275 a brief exposure to less severe cold or high temperatures (rapid cold/heat hardening)
276 (Denlinger *et al.*, 1991). It is associated with the expression of heat shock proteins or stress
277 proteins (hsp), which protect organisms from heat/cold shock by stabilizing and preventing the
278 aggregation, and improper folding of proteins (Denlinger *et al.*, 1991; Fields *et al.*, 1998; Beckett
279 *et al.*, 2007). In pest-control applications, there is little evidence suggesting that heat-
280 acclimation has any practical significance at temperatures used for control, 50-60°C (Evans,
281 1987). At low temperatures, rapid rates of cooling prevent acclimation, which otherwise can
282 increase survival by 2- to 10-fold (Evans, 1987; Fields, 1992; Beckett *et al.*, 2007). For *T.*
283 *variabile*, cold-acclimated diapausing larvae are much more cold-tolerant than non-acclimated
284 diapausing larvae (Abdelghany *et al.*, 2015).

285 **3.6 Temperature and duration of exposure**

286 The level of mortality experienced by insects at a given temperature is a function of the
287 duration of exposure (Salt, 1958; Fields, 1992; Strang, 1992; Linnie, 1999). The relationship is

288 normally determined experimentally to calculate the combination of temperature and duration
 289 needed to kill a given percentage of the population (Fields, 1992; Fields & White, 2002;
 290 Eliopoulos *et al.*, 2011). In *T. variable*, 100% of non-diapausing larvae are killed after 17 days of
 291 exposure to -5°C compared to 1 day at -20°C (Table 2) (Abdelghany *et al.*, 2015).

292 **Table 2.** Time necessary to reach mortality at sub-zero temperatures for different species of
 293 economically important dermestid beetles.
 294

Species	Reference	Life stage	Accli- mation	Tempe- rature (°C)	Duration	Mor- tality (%)
<i>Trogoderma granarium</i>	Lindgren & Vincent (1959)	Starved larvae	-	-10 to -7	36 d	40
		Fed larvae	-	-10 to -7	36 d	100
	Mathlein (1961)	Larvae	Yes	-2	180 d	45
				-5	90 d	23
				-10	30 d	97
				-19	15 d	100
					10 d	100
	Solomon & Adamson (1955)	Larvae	-	-3 to -8	10 mo	<4
	Voelkel (1924) cited in Hinton, 1945	Larvae	Yes	-10	72 h	11
			No	-10	25 h	73
			No	-16	24 h	98
			No	-16	16 h	100
	Eliopoulos <i>et al.</i> , (2011)	Young larvae	-	-16	4 h	100

Species	Reference	Life stage	Acclimation	Temperature (°C)	Duration	Mortality (%)
		Old larvae		-16	24 h	95
		Young adult		-16	12 h	92
		old adult		-16	12 h	97
	Zacher (1938) cited in Strang (1992)	Larvae 4th instar	-	-10	25 h	50
	Reynolds & Rundle (1967)	Larvae	No	-10	0 - 3.5 h	3
					7.5 - 41 h	76
					48 - 72 h	91
	Wilches <i>et al.</i> , (2014)	Eggs, Pupae, Adults	No	-10	20 d	100
		Larvae	No	-10	7 d	45
		Diapausing larvae	No	-10	7 d	25
<i>Trogoderma variabile</i>	Abdelghany <i>et al.</i> , (2015)	Eggs	No	0	4 d	95
		Larvae	No	0	32 d	95
		Larvae	Yes	0	240 d	95
		Diapausing larvae	No	0	53 d	95
		Diapausing larvae	Yes	0	>275 d	50
		Larvae	No	-5	17 d	100
				-10	10 d	100
				-15	6 d	100

Species	Reference	Life stage	Acclimation	Temperature (°C)	Duration	Mortality (%)
				-20	1 d	100
		Diapausing larvae	Yes	-5	175 d	100
				-10	100 d	100
				-15	49 d	100
				-20	25 d	100
		Pupae	No	0	25 d	95
		Adults	No	0	15 d	95
<i>Trogoderma inclusum</i>	Reguzzi <i>et al.</i> , (2011)	All life stages	No	-22	3 h	100
		Larvae	Yes	-22	3 h	90
		Adults	No	-10	5 h	95
		Eggs, larvae, pupae	No	-10	6 h	100
<i>Trogoderma angustum</i>	Bergh <i>et al.</i> , (2006)	Larvae	No	-20	3 d	95
<i>Attagenus fasciatus</i>	Ali <i>et al.</i> , (1997)	Pupae	-	-5	7 h	100
		Pupae		0	6 d	100
<i>Attagenus pello</i>	Florian (1986)	Eggs	-	-18	4 h	100
<i>Attagenus smirnovi</i>	Bergh <i>et al.</i> , (2006)	Larvae	No	-20	1 d	100

Species	Reference	Life stage	Acclimation	Temperature (°C)	Duration	Mortality (%)
				-14	1 d	100
				-12	1 d	98
<i>Attagenus unicolor</i>	Back & Cotton (1926) cited in Strang (1992)	Larvae	-	-4	198 d	100
	Salt (1936)	Larvae	-	-22	several min	100
		Pupae/adults		-24	several min	100
<i>Attagenus woodroffeii</i>	Bergh <i>et al.</i> , (2006)	Larvae	No	-20	1 d	100
<i>Anthrenus verbasci</i>	Linnie (1999)	All life stages	-	-20	3 h	100
		Eggs, adults		-10	3 h	100
		Larvae		-10	24 h	10
		Pupae		-10	24 h	80
	Arevad (1979)	Eggs/pupae/adults	-	-20	2 h	100
	Bergh <i>et al.</i> , (2006)	Larvae	No	-20	1 d	93
<i>Anthrenus museorum</i>	Arevad (1974) cited in Strang (1992)	Larvae	-	-20	2h	<100
	Arevad (1979)	Adults	-	-20	1 h	100
		Eggs		-20	6 h	100

Species	Reference	Life stage	Acclimation	Temperature (°C)	Duration	Mortality (%)
	Bergh <i>et al.</i> , (2006)	Larvae	No	-20	3 d	70
<i>Anthrenus flavipes</i>	Back & Cotton (1926) cited in Strang (1992)	All life stages	-	-18	1 d	100
<i>Dermestes vorax</i>	Dawson (1984) cited in Strang (1992)	Larvae	-	-15	6 d	100
<i>Dermestes maculatus</i>	Strang (1992)	All life stages	-	-23	6 h	100
	Linnie (1999)	Eggs	-	-10	6 h	100
		Larvae, Pupae		-10	24 h	< 35
		Adults		-10	9 h	100
		All life stages		-20	3 h	100
	Zhang (2012)	Adults	No	-20	6 h	100
<i>Reesa vespulae</i>	Bergh <i>et al.</i> , (2006)	Larvae	No	-20	3 d	100
		Larvae		-20	1 d	80
	Mehl (1975) cited in Strang (1992)	Larvae	-	-20	2 d	>90
		Larvae		-10	14 d	>90
	Arevad (1974) cited in Strang (1992)	Larvae	-	-20	1 h	>90

295 *Blank cells represent unavailable information

296 **4. CONTROL OF DERMESTIDS WITH EXTREME TEMPERATURES**

297 Extreme high and low temperatures are becoming more widely used to eradicate infestations
298 of dermestids in storage facilities and museum collections (Bergh *et al.*, 2006). However, most
299 dermestid species can enter diapause (Table 1), which may increase their tolerance to extreme
300 temperatures (Fields, 1992; Bell, 1994). Thus, successful application of extreme temperatures
301 requires information on the mortality of given species under different combinations of
302 temperatures and durations, and consideration of how factors such as diapause or acclimation
303 affect thermal tolerance (Burges & Burrell, 1964; Strang, 1992; Fields, 2001).

304 In the following sections, we briefly report on the literature pertaining to the thermal tolerance
305 of dermestids. Relevant papers initially were identified with key word searches in the databases
306 SCOPUS, Google Scholar, Research Gate, and Science Direct. The key words used for these
307 searches were low temperatures/ high temperatures, control, Dermestidae (or each of the
308 genera of economic interest). Additional papers, mainly published prior to 1960, were identified
309 by examining references cited in more recently published papers. Papers not published in
310 English were not considered.

311 **4.1 Low temperature**

312 We identified 23 papers pertaining to the survival of economically-important dermestid beetles
313 at low temperatures (Table 2). Seven of these were published since 2005; the remainder were
314 either published prior to 1980. The greatest quantity of information was found for *T. granarium*
315 larvae held at -10°C. Depending upon the study, mortality of > 95% is achieved after 30 d of
316 exposure (Lindgreen & Vincent 1959; Mathlein 1961), of 91% after 72 h (Reynolds & Rundle,
317 1967), of 73% (Voelkel, 1924 cited in Hinton, 1945) and 50% (Zacher, 1938 cited in Strang, 1992)
318 after 25 h. This variation may be due to use of different methods (Fields, 1992; Zhang, 2012).

319 Many studies provide little or no information on whether larvae were acclimated or in
320 diapause, how the data were analysed, or on confidence limits to assess the variation in
321 responses among individuals.

322 Only six studies have assessed the effect of acclimation and diapause on cold-tolerance.

323 Lindgreen & Vincent (1959) showed that starvation reduced the mortality of *T. granarium*

324 larvae held for 36 days at -10 °C (Table 2). These starving larvae were likely in diapause (Burges,

325 1960). Three studies report an acclimation protocol before exposing the larvae of *T. granarium*
326 (Voelkel, 1924 cited in Hinton, 1945), *T. inclusum* (Reguzzi *et al.*, 2011) and *T. variabile*
327 (Abdelghany *et al.*, 2015) to sub-zero temperatures. Results of these studies indicate that
328 acclimation enhances survival at low temperatures (Table 2). Only one study reported on how
329 the combined effect of diapause and acclimation affected temperature tolerance. In a study on
330 *T. variable*, Abdelghany *et al.*, (2015) showed that the two factors were synergistic, with
331 acclimation being the main factor that increases cold-tolerance in this insect.

332 Variation among studies confounds the detection of general patterns (Table 2). The larval
333 stages appear to be the most cold-tolerant in the majority of dermestid species, particularly for
334 *T. granarium* (Mansbridge, 1936; Solomon & Adamson, 1955). To achieve > 90% mortality for
335 larvae held at -10°C, 30 days is required for *T. granarium* (Mathlein 1961), compared to 6 h for
336 *T. inclusum* (Reguzzi *et al.*, 2011).

337 Low temperatures are more likely than high temperatures to be used in thermal treatments for
338 pest control because, although longer exposure is needed to reach mortality, they are less likely
339 to damage the treated product (Evans, 1987; Linnie, 1999). On products with low moisture
340 content, temperatures as low as -29°C have little effect on product quality but, in most
341 products, too-high temperatures can lead to deleterious chemical and biochemical changes and
342 most of these depend on the way the heat is delivered (Evans, 1987). Avoiding damage to the
343 product requires studies specific to the product to determine the combination of temperature
344 and duration exposure needed to achieve control, followed by post-treatment studies to assess
345 product quality (e.g., for processed foods, preserved specimens, textiles) or viability (e.g., for
346 bulk seeds) (Burges & Burrell, 1964; Evans, 1987; Fields, 1992; Fields *et al.*, 2012).

347 **4.2 High temperature**

348 We identified 24 papers reporting on the control of dermestids with high temperatures (Table
349 3). The most recent of these was published in 2002 (Wright *et al.*, 2002), only two of the studies
350 considered the effect of diapause, and no studies assessed the effect of acclimation on heat-
351 tolerance. The rarity of such studies is likely because diapause does not typically increase
352 survival at temperatures used for heat treatments (50-60°C) (Evans, 1981). Wright *et al.* (2002)

353 reported that diapause does not increase heat tolerance in larvae of *T. variabile* held for 4
 354 minutes at 56°C. However, Battu *et al.*, (1975) reported the need of a longer exposure time at
 355 50°C to reach 95% mortality in *T. granarium* larvae in diapause (20 h) compared to non-
 356 diapausing larvae (5.3 h).

357 **Table 3.** Time necessary to reach >90% mortality at high temperatures for different species of
 358 economically important dermestid beetles, no beetles in these studies were acclimated.
 359

Species	Reference	Life stage	R.H. (%)	Temperature (°C)	Duration	Mortality (%)
<i>Attagenus scalaris</i>	Abdel-Rahman <i>et al.</i> , (1981)	Larvae	-	50	35 min	100
<i>Attagenus fasciatus</i>	Ali (1997)	Pupae	-	45	18 h	100
				50	30 min	100
	Ali (1992)	Larvae	-	50	20 min	100
<i>Attagenus pellio</i>	Zacher (1927) cited in Strang (1992)	Eggs/larvae	-	52	20 min	100
<i>Anthrenus verbasci</i>	Linnie (1999)	All life stages	-	50	6 h	100
<i>Anthrenus flavipes</i>	Ayappa <i>et al.</i> , (1957)	Pupae	30	41	2 h	100
			90	41	1 h	100
<i>Anthrenus coloratus</i>	Ali (1997)	Larvae	-	50	12 min	100
<i>Anthrenus sarnicus</i>	Armes (1985) cited in Linnie (1999)	All life stages	-	40	2 h	>90

Species	Reference	Life stage	R.H. (%)	Temperature (°C)	Duration	Mortality (%)
<i>Dermestes maculatus</i>	Nakayama <i>et al.</i> , (1983)	All life stages	-	50	30-60 min	>90
	Linnie (1999)	All life stages	-	50	3 h	100
<i>Dermestes coarctatus</i>	Yokoyama (1927) cited in Strang (1992)	Larvae/pupae/adults	-	50	1 h	100
				55	15 min	100
<i>Trogoderma granarium</i>	Battu, <i>et al.</i> , (1975)	Diapausing larvae	70	42	16 d	95
				45	6 d	95
				50	20 h	95
				42	13 d	95
				45	4.2 d	95
				50	5.3 h	95
	Husain & Bhasin (1921)	Larvae	-	50	5 h	>90
				54	20 min	>90
				60	4 min	>90
	Lindgren & Vincent (1959)	Eggs	-	57	3 min	95
	Lindgren <i>et al.</i> , (1955)	All life stages	75	55	8 min	95

Species	Reference	Life stage	R.H. (%)	Temperature (°C)	Duration	Mortality (%)
			95	55	15min	95
	Fleurat-Lessard (1985)	larvae	-	70	16 sec	100
	Ismail <i>et al.</i> , (1988)	All life stages	-	60	30 min	100
	Taheri (1988)	All life stages	-	45	4 d	100
	Mookherjee <i>et al.</i> , (1968)	Pupae	-	50	16 h	100
	Saxena, <i>et al.</i> , (1992)	Pupae	-	45	48 h	84
				55	2 h	100
	Shoab (2009)	Larvae	-	60	2 min	100
		Larvae		57	5 min	100
		Larvae		54	12 h	100
		Larvae		51	48 h	100
	Zacher (1927) cited in Strang (1992)	Larvae	-	50	5.6 h	>90
				52	1.5 h	>90
				53	0.5 h	>90
				54	20 min	>90
				55	10 min	>90
				58	5 min	>90
				71	1 min	>90
				82	0.5 min	>90

Species	Reference	Life stage	R.H. (%)	Temperature (°C)	Duration	Mortality (%)
	Wilches <i>et al.</i> , (2014)	Eggs, Pupae, Adults	-	45	7 d	>90
<i>Trogoderma variabile</i>	Wright <i>et al.</i> , (2002)	Egg	0	56	4 min	98.6
		Small larvae			2 min	91
		Large larvae			4 min	100
		Diapause larvae			4 min	93.3
		Pupae			4 min	100
		Adult female			4 min	96.4
	Kirkpatrick & Tilton (1972)	Adults	-	40	>24 h	>90
			45	12 h	>90	
			50	5 min	>90	
			55	1 min	>90	

360

361 *Blank cells represent unavailable information

362

363 The mechanisms of mortality are similar between extreme temperatures and desiccation,
364 adaptations to dehydration may enhance temperature tolerance (Danks, 1996, 2000). Insects
365 adapted to tolerate dry environments will likely be able to better tolerate extreme temperatures
366 (Danks, 1996, 2000). *Trogoderma granarium* and *A. verbasci* appear to be the most heat-
367 tolerant of the dermestids (Table 3). When held at 50°C, exposure for more than 5 h is required
368 to achieve >90% mortality for these species; whereas a similar level of mortality can be
369 achieved within minutes for other dermestid species. The result of *T. granarium* being more

370 heat-tolerant is not unexpected, given that it is endemic to hot and dry environments (Hinton,
371 1945; Banks, 1977; Eliopoulos, 2013). In contrast, *T. variable*, which has a Nearctic origin (Table
372 1), seems to be less heat-tolerant, reaching >90% mortality in less than 5 minutes at 50°C
373 (Kirkpatrick & Tilton, 1972; Wright *et al.*, 2002). Studies on *A. flavipes* and *T. granarium* also
374 suggest that relative humidity (rh) plays an important role in heat tolerance and when
375 increased, it might increase heat tolerance (Lindgren *et al.*, 1955; Ayappa *et al.*, 1957)

376 Within the dermestids, *T. granarium* is among those that have greatest thermal tolerance such
377 that temperature treatments sufficient for its control would likely suffice for other species
378 (Howe, 1965; Fields, 1992). In general, the published literature indicates that dermestid species
379 cannot survive exposures of more than 3 days at temperatures below -20°C or more than 2
380 hours above 50-60°C (Table 3). Future studies to control dermestids at high and low
381 temperatures must include different life stages of the insect, a wide range of temperatures and
382 exposure times, and standardization of the analytical methods to determine the lethal time for
383 the 50 and 95% of the population (LT₅₀ and LT₉₅). The most widely used regression nowadays is
384 the probit regression, which must be used only when the mortality vs time data follows a
385 sigmoidal shape and should be reported with its variance estimates (fiducial limits) in order to
386 be comparable (Fields, 1992).

387 **4.3 Models**

388 Mathematical models can be used to design effective thermal treatments for pest control. Such
389 models require data on the survival of a species at different combinations of temperature and
390 duration of exposure. Such data are normally obtained in laboratory studies for the most cold-
391 /heat-tolerant life stage, including stages in diapause (Fields, 1992; Abdelghany *et al.*, 2015).
392 Mortality of insects under constant temperatures can be modeled using kinetic or empirical
393 models; e.g., modified fundamental kinetic and modified complementary log-log
394 transformation models (Jian *et al.*, 2010). Mortality can be modelled as a function of time
395 required for the facility to reach the lethal temperature, the duration required for exposure to
396 that lethal temperature, and the maximum/minimum temperature required for mortality
397 (Subramanyam *et al.*, 2011). Mathematical models also have been developed for the use of

398 non-constant temperatures to control stored product pests; e.g., heat accumulation model and
399 heat treatment zones model (Jian *et al.*, 2013). Application of existing models may be condition
400 dependent. Hence, models may require validation for a given combination of species,
401 temperature range, and site (e.g., building, container, and product) of application (Jian *et al.*,
402 2010).

403 Models also can be developed to predict the risk of future global spread and establishment for
404 a given insect pest (Paini & Yemshanov, 2012). This can be done with species occupancy
405 models, by identifying the optimal temperature and humidity for the pest development,
406 reproduction and survival, and then matching this information to geographic regions where the
407 pest does not yet occur (Banks, 1977). Such models have been developed for *T. granarium*,
408 which is a major pest of stored grains and a quarantine pest in Canada, USA, and Australia
409 because, if introduced and (or) established into these countries it would cause high economic
410 losses. Paini & Yemshanov (2012) assessed the risk of *T. granarium* arriving in Australia using a
411 first-order Markov chain model. This model used information on *T. granarium*'s current
412 distribution and the probability of its presence in countries where it has not yet been reported,
413 to determine the most likely source countries and ports of entry into Australia. Previous studies
414 indicate that *T. granarium* requires conditions of $> 20^{\circ}\text{C}$ average temperature for at least four
415 months in a year to establish and reach pest status (Hadaway, 1955; Howe & Lindgren, 1957).
416 Based on this information, mathematical models predict that *T. granarium* is unable to
417 establish anywhere in Canada, except possibly in heated storage facilities (Ameen, 2012).
418 However, these models may need to be reassessed, given new information on the thermal
419 tolerance of cold-acclimated insects or insects in diapause, plus a general warming of
420 temperatures in recent decades due to climate change (Estay *et al.*, 2009).

421 **5. Conclusions**

422 The development of protocols using extreme temperatures to control dermestids is hindered
423 by a general lack of information on the thermal tolerance of acclimated individuals, and on
424 individuals in diapause. Diapause research on dermestids can be difficult, because of the high
425 degree of ecological plasticity among species and the diverse physiological and environmental

426 cues that trigger diapause induction (Table 1) (Bell, 1994; Zhantiev, 2009). Species exhibiting
427 density-dependent diapause may be particularly good models to study the effects of diapause
428 on thermal tolerance, because diapause induction is independent of temperature and,
429 therefore, is not confounded by temperature acclimation (Nair & Desai, 1972; Abdelghany,
430 2015).

431 The diapause stage in dermestids makes their control difficult and enhances the pest status of
432 some species. Diapause allows these insects to use an intermittent food supply and survive
433 adverse conditions such as low temperature or the application of insecticides. The factors and
434 their magnitude necessary to induce and terminate diapause must be clearly identified in order
435 to manipulate diapause and develop more effective methods of pest control for dermestids.
436 Although it has not been greatly assessed, diapause together with acclimation can increase
437 significantly the temperature tolerance of dermestids (Fields, 1992; Abdelghany *et al.*, 2015).
438 Studies on the development of strategies and models to control dermestid species should
439 include the study of diapause and acclimated larvae of each species. Larvae under these
440 conditions are likely the most resistant to the method of control (Burges, 1962b; Wright &
441 Cartledge, 1994; Denlinger, 2008).

442 This review shows that from the practical point of view our knowledge about heat/ cold-
443 tolerance on dermestid beetles is fragmentary and the methods used are not very rigorous or
444 standardized. Future studies should, in particular, identify triggers for induction and
445 termination of diapause, and develop methods to better identify diapausing individuals. The
446 clear identification of other factors inducing and terminating diapause may lead to the
447 manipulation of environmental conditions to prevent induction of the tolerant diapausing stage
448 and the success of control methods such as the use of extreme temperatures (Nair & Desai,
449 1972; Wright & Cartledge, 1994; Kostál, 2006). Studies on extreme temperatures needed for
450 control of dermestid pests should consider factors such as species and life stages to be
451 exposed, rates of cooling and heating, well specified environmental conditions used in the
452 experiment besides details of mathematical analyses used and the consideration of the
453 mortality at various temperatures to be used in mathematical modelling of the control method.

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